

THE LATE PRECAMBRIAN FOSSILS FROM EDIACARA, SOUTH AUSTRALIA

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ABSTRACT. New genera and species are described from the richly fossiliferous Late Precambrian strata in which a number of medusoid fossils were discovered by R. C. Sprigg in 1947 and from which various pennatulacean, annelid, and other fossils have been described since. The new genera and their type species are: *Medusinites asteroides* (Sprigg), *Mawsonites spriggi* sp. nov., *Conomedusites lobatus* sp. nov., *Lorenzinites rarus* sp. nov., *Kimberia quadrata* sp. nov., *Rugoconites enigmaticus* sp. nov., *Arborea arborea* (Glaessner), *Oyatoscutum concentricum* sp. nov., *Praecambrium sigillum* sp. nov. In addition, the new species *Cyclomedusa plana*, *Rangea longa*, *R. grandis*, *Dickinsonia elongata*, *D. tenuis*, and *Spriggina? ovata* are described. The synonymies of several genera and species are revised, and new morphological information on others, particularly *Tribrachidium heraldicum* Glaessner, is presented.

SINCE the first accounts of the discovery of new Late Precambrian fossils at Ediacara were published (Glaessner 1958, 1959*a, b*, 1960, 1961, 1962; Glaessner and Daily 1959), much interest in this fauna has been expressed in the literature, in discussions, in the form of requests for illustrations for publication in a great variety of books, and in many other ways. Collecting and indexing of specimens from this locality, now numbering over 1,400, was continued and the authors have carried out jointly their study and interpretation. A comprehensive publication on the accumulated material is in preparation. It will deal with its geological aspects, fossilization, systematics, biological, evolutionary, and biostratigraphic interpretations. Nine new genera and thirteen new species are described, the synonymy of others has been altered, and new material of some known species has revealed additional important characters. Some of these new data are now made available to those interested in the early history of metazoan evolution and relationships, pending completion of more comprehensive investigations.

The description of this unusual collection of remains of soft-bodied animals preserved in hard sandstone or quartzite requires a careful consideration of the circumstances of their fossilization so as to discriminate, as far as possible, between results of post-mortem alterations and original morphological characters. The general sedimentary environment of the Ediacara fauna can be described as shallow marine and littoral. The position of the shoreline at the time when deposition of the Pound Quartzite in the Adelaide Geosyncline and on its western shelf margin was about to end is not known. Occasional emergence of sandy shoals is proved by the occurrence of networks of drying cracks on some bedding planes of the fossiliferous strata. The sediment is dominantly arenaceous; cross-stratification indicates moving sand ripples, and ripple-marked bedding planes are common. In this environment the fossils would not have been preserved but for one important local feature. The sandstone, now partly altered to quartzite, is flaggy, and the sandy layers are separated by argillaceous laminae and thin lenses. They represent areas of temporary quiescent conditions between the shifting current tracks, where fine particles could settle until they were covered again by sand waves. The animal remains which came to rest on the muddy or silty flats and pool bottoms either made impressions in the sediment or were retained there bodily until covered with sand by the next shifting

current. The sand, though partly coarse, must have had some of the qualities of a foundry sand to be able to produce more or less perfect casts and moulds of the underlying sediment surface and of the animal moulds, tracks, and remains on it. The clay lenses were subsequently highly compacted and altered and are now mostly only thin, lenticular partings between the quartzite flags. Most of these partings can be opened only by natural weathering. They reveal fossils mostly on the lower surfaces of the quartzite flags. The upper portions of the sandy sedimentation units had apparently only rarely the required composition and consistency to retain them.

This peculiar mode of fossilization, which explains the localization of fossils along a few miles of outcrop of a stratigraphic horizon which has now been mapped regionally over hundreds of miles, requires careful consideration of its implications for descriptive work. Existing terminology must be applied with care to the five observed states of preservation of these fossils. Most of the medusoid remains are preserved in the form of a flattened convex *cast* (1) on the lower surface of a quartzite slab of the original depression in the underlying sediment. Sand-filled hollows or decayed parts of the organisms are also preserved as casts but these are rare. The depression in the underlying stratum which corresponds to the cast is its *counterpart mould* (2) which reproduces the surface features of the cast as its mirror image. A superimposition of the features of the lower surface of the organism (as deposited), moulded on the underlying stratum, and of those of its upper surface, produces a *composite mould* (3) (McAlester 1962). Where a convex feature on the underlying surface, possibly the dead organism itself, is impressed into the lower surface of the overlying stratum, we speak of an impression or *external mould* (4). The corresponding natural cast of this impression which is occasionally seen on a sandy bed below is the *counterpart cast* (5). It will be noted in the systematic part that two of the genera here described as medusoid are known as external moulds, as are all known representatives of the genera *Spriggina*, *Parvancorina*, and *Tribrachidium*, though in the last genus one external mould of the lower surface is known, in addition to those of the upper surface of this and many other specimens. Uncertainties in the distinction between the two sides of flat bodies which are caused by these modes of preservation add to the difficulties of their morphological and functional analysis. The preferential preservation as casts or external moulds in various taxonomic groups can be seen as a function of their resistance to decay or of the toughness of their tissues. Fortunately, with very few exceptions, each species is represented by many specimens, so that accidents of fossilization can be recognized by comparison.

At the present stage of our inquiries we do not wish to introduce any suprageneric classifications. The medusoid fossils cannot be generally classified into Scyphozoa and Hydrozoa, though comparisons suggest that both taxa are represented. The two annelid genera described clearly belong to two widely different families, but the level of their separation will not be discussed here.

The geology of the Ediacara area has been the subject of very detailed studies by geologists of the South Australian Mines Department who have carried out a geochemical investigation of the metalliferous Lower Cambrian carbonate rocks at this locality. In the course of this work (Nixon 1963, 1964) the fossiliferous strata of the Pound Quartzite and the overlying Parachilna Formation (Dalgarno 1964) were mapped in detail.

For reasons which have been stated (Glaessner 1960, 1962, 1963*b*; H. and G. Termier

1960) the Ediacara fauna is considered as Late Precambrian, preceding stratigraphically and chronologically the appearance of the first known Lower Cambrian faunas. South Australian geologists have accepted this designation in their regional mapping. The composition of the fossiliferous formation makes it unlikely that it will ever be dated directly by radioactivity methods.

The fauna as known at present comprises the following 25 species. There are indications of the presence of additional species and of trace fossils which require further study.

Phylum Coelenterata

A. Medusoid

- Ediacaria flindersi* Sprigg
- Beltanella gilesi* Sprigg
- Medusinites asteroides* (Sprigg)
- Cyclomedusa davidi* Sprigg
- C. radiata* Sprigg
- C. plana* sp. nov.
- Mawsonites spriggi* gen. et sp. nov.
- Conomednsites lobatus* gen. et sp. nov.
- Lorenzinites rarus* gen. et sp. nov.
- Pseudorhizostomites howchini* Sprigg
- Rugoconites enigmaticus* gen. et sp. nov.
- Kimberia quadrata* gen. et sp. nov.
- Ovatoscutum concentricum* gen. et sp. nov.

B. Pennatulacean

- Rangea longa* sp. nov.
- R. grandis* sp. nov.
- Pteridinium* cf. *simplex* (Gürich)
- Arborea arborea* (Glaessner)

Phylum Annelida

- Dickinsonia costata* Sprigg
- D. elongata* sp. nov.
- D. tenuis* sp. nov.
- Spriggina flouderesi* Glaessner
- S.?* *ovata* sp. nov.

Phylum uncertain

- Praecambrium sigillum* gen. et sp. nov.
- Parvancorina minchani* Glaessner
- Tribraclidium heraldicum* Glaessner

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Cambridge facilitated the completion of this paper. The text figures were re-drawn by Miss M. Boyce (Adelaide). To all those who helped in this investigation we express our sincere thanks.

Depositories. Registered numbers prefixed P refer to specimens deposited in the South Australian Museum. Those prefixed T or F refer to specimens in the Geology Department, University of Adelaide.

SYSTEMATIC DESCRIPTIONS

Phylum Coelenterata

A. Medusoid fossils

Most of the medusoid fossils from Ediacara are preserved as more or less flattened convex casts on the lower surfaces of quartzite beds. In this preservation, a medusa could show the shape of the exumbrellar surface and often also remains of any marginal flange which, if present, could either spread around the entire periphery, or part of it, or it could be hidden under the body. Such a cast could also show the subumbrellar side on which one would expect oral or gastric structures, and a velum impression in hydroid medusae. Actually, no clearly defined structures of this kind have been seen since Sprigg (1947, 1949) interpreted in this manner some of the fossils described by him. The distinction between preservation of the exumbrellar or subumbrellar surface is not necessarily clear-cut, as a number of the medusoid fossils show signs of composite moulding of parts of both surfaces. It is possible that in some of them remains of radial grooving which do not reach the centre are to be considered as subumbrellar, while most of the concentric grooving, particularly in the central part, was exumbrellar. Gradual decay of the gelatinous bell during fossilization introduces further complications. It is more important to recognize the complexities of structural interpretation of ancient medusoid fossils than to attempt prematurely their placing in the existing system. Further comparative studies are required but some distinctive genera and species are here recorded.

Genus EDIACARIA Sprigg 1947

Type species. *Ediacaria flindersi* Sprigg 1947.

Characters as for type species.

Ediacaria flindersi Sprigg 1947

Plate 99, fig. 6

- 1947 *Ediacaria flindersi* Sprigg, p. 215, pl. 5, figs. 1, ?2, text-fig. 3.
- 1949 *Ediacaria flindersi* Sprigg, p. 83, pl. 10, fig. 2, text-fig. 5.
- 1949 *Madigania annulata* Sprigg (*partim*), p. 93, pl. 17, figs. 1, 2 (*non* pl. 16, figs. 1, 2).
- 1949 *Protodipleurosoma wardi* Sprigg, p. 79, pl. 9, fig. 2, text-fig. 3E.
- 1956 *Ediacaria flindersi* Sprigg (*partim*), *Protodipleurosoma wardi* Sprigg; Harrington and Moore, *in* Moore, p. F74, fig. 60 (1); p. F79, fig. 64.
- 1959 *Ediacaria flindersi* Sprigg; Glaessner, *in* Glaessner and Daily, p. 378.
- 1962 *Ediacaria* Sprigg; Glaessner, p. 483.

Material and preservation. Over 40 specimens are definitely assigned to this species, while 30 small specimens, 3 relatively uncompressed specimens, 5 composite moulds with rather strong radial furrows, and a number of fragments may belong here.

Most specimens are rather flat composite moulds dominated by exumbrellar structures but some are gently domed. Strong radial furrows on some specimens may indicate subumbrellar structures.

The species was gregarious; one slab measuring about 45 × 30 cm. bears parts of 9 specimens with radii from 30–120 mm.

Holotype. T1–2058.

Dimensions. This is the largest medusoid known from Ediacara. The largest complete specimen has a mean radius of 120 mm. but a fragment has a radius of 210 mm. and another fragment indicates a much larger specimen. The holotype has a mean radius of 50 mm.

Diagnosis. The surface (which is considered as exumbrellar) shows a central disc and an outer ring, without any marginal flange. The disc is often slightly elevated above the outer ring. The surface of the disc may be marked by a sharp annular furrow which does not necessarily run parallel with its outer boundary. It could indicate the edge of the gastric cavity. Some specimens show additional concentric grooves on the disc. Several of them may be grouped close to the centre. Arcuate folds marked by grooves parallel to the periphery may also occur on the outer ring. Radial furrows are mostly confined to it but they are not present in all specimens. Crenulations of the periphery are probably accidental. The radius of the central disc is from one-quarter to three-quarters of the total radius.

Remarks. One-quarter of the holotype is poorly preserved and superimposed on a small *Cyclomedusa* near the centre. This *Cyclomedusa* has caused distortion, straightening the annular furrows near the centre of the *Ediacaria*. It may be the sole cause of some of the straight furrows delimiting one side of the subtriangular structure which Sprigg (1949, p. 85) interpreted as a manubrium. The other furrows delimiting this structure are a radial and a concentric furrow, each in line with the normal furrows of the disc but exceptionally deep.

Sprigg (1947, 1949) described 'three pendant pouches extending radially from the base of the manubrium' in the position in which Harrington and Moore (*in* Moore 1956, p. F75) noted four 'circular knobs'. One or two of these irregularities appear to be due to distortion by the *Cyclomedusa* and the specimen does not support clearly either of the quoted descriptions. The outer ring shows a number of partial concentric folds. The general morphology of a more corrugated outer ring and a smoother, more convex disc, both with a surface texture of fine, radial striae, indicates that this specimen is an exumbrellar surface. None of the radial or concentric markings on the central disc can be attributed with any probability to internal or subumbrellar structures. Many radial furrows occur near the margin of the outer ring but less than half of them cross it. Most of those that do, die out at the edge of the central disc but a few reach to, or just across, a partly doubled annular depression on the disc which Sprigg (1947) regarded as the outer edge of the 'gastrovascular cavity' or 'stomach'. The radial depressions on the outer ring of the holotype are more numerous than those in any other specimen interpreted as an exumbrellar surface. They are deeper and less numerous than those on the subumbrellar surfaces tentatively assigned to *Ediacaria* (Sprigg 1947, pl. 5, fig. 2, and other specimens). There is very little branching or overlapping of the radial furrows despite the striking arrangement of canals drawn in restorations (Sprigg 1947, text-fig. 3A, B; 1949, text-fig. 5A–C).

The holotype of *Protodipleurosoma wardi* Sprigg (1949, pl. 9, fig. 2) is a composite mould. All its exumbrellar characteristics are those of *Ediacaria flindersi*. It differs in the relatively small size and elongate-oblate shape of the sharp furrow that may indicate

its gastric cavity (Sprigg 1949, p. 79). The enclosed portion is slightly elevated as if the area had been filled with sand before compression. Groups of furrows radiate from opposite points. They are deepest adjacent to the sharp furrow, and shallow away from it. There is also a fine wrinkling across the surface with which the constriction across the 'stomach' shown by Sprigg (1949, text-fig. 3E) is associated. These furrows and wrinkling are probably both compressional features due to the flattened infilling of sand; there are no structures equivalent to them among the new specimens of medusoid fossils. Thus the 'radial canals' (Sprigg) are not a convincing taxonomic character. The study of '*Protodipleurosoma wardi*' shows that several partial concentric folds have been aligned as a ring canal in Sprigg's text-fig. 3E, while the new material of *Ediacaria* shows that the development of concentric furrows on the outer ring, varying in completeness and number, is common. The centre of the disc, where the area within the oblate furrow is least raised, shows faintly a small, circular structure such as is seen on many specimens of *Ediacaria*. The size of the infilled area is the only remaining distinction between *Protodipleurosoma* and *Ediacaria*. This character cannot be considered as taxonomically distinctive. *Protodipleurosoma wardi* Sprigg 1949 appears to be a composite mould of *Ediacaria flindersi* Sprigg 1947, and the name is suppressed as a junior synonym.

Genus BELTANELLA Sprigg 1947

Type species. *Beltanella gilesi* Sprigg 1947.

Beltanella gilesi Sprigg

- 1947 *Beltanella gilesi* Sprigg, p. 218, pl. 6, fig. 1, text-fig. 4A-C.
 1949 *Beltanella gilesi* Sprigg; Sprigg, p. 81, pl. 10, fig. 1, text-fig. 4D-F.
 1956 *Beltanella gilesi* Sprigg; Harrington and Moore, in Moore, p. F70, fig. 56.
 1959 *Beltanella gilesi* Sprigg; Glaessner, in Glaessner and Daily, p. 378.
 1962 *Beltanella* Sprigg; Glaessner, p. 483, pl. 1, fig. 3.

Holotype. T3-2056.

Description. The holotype is a convex cast, highest at one side of the central disc. The type figure (Sprigg 1947; reproduced by Sprigg 1949, Harrington and Moore in Moore 1956) shows three bosses regularly spaced near the margins of the central disc; these are the clearest, but alternative lighting (Glaessner 1962) shows a fourth boss between and to the centre from two others. This distorts the concentric furrow which occurs at mid-radius of the central disc. In the possession of these bosses *Beltanella gilesi* remains unique but its other characteristics are shared by several specimens which cannot be separated from *Ediacaria flindersi*.

Its outer flange appears narrower than the outer ring of *Ediacaria*; it is only 5-7 mm. wide over one-half of the circumference of *Beltanella*, but it widens out to a width of 13 mm. where the total radius is 56 mm. Even here, concentric folds show that it was not stretched. The mean diameter of the central disc is just over 80 mm., so that the proportions of this apparent 'outer flange' fall within those of the 'outer ring' of *Ediacaria*. Similarly, the central disc is fairly smooth, bearing a concentric furrow (here partly double) at mid-radius. The central structure is delimited by four annular furrows, the outer 12 mm. and the inner 4 mm. in mean diameter. It consists of two flat rings, each 1 mm. across, and a narrower inner ring; probably the innermost portion was a

boss but it is now broken and a sharp-edged depression occupies the centre. The natural features of this central structure can be closely matched among the available material of *Ediacaria*. A structure that is not matched among the *Ediacaria* specimens is the double radial furrow delimiting a low ridge, which crosses from the outer edge of the central disc to the concentric furrow at mid-radius of the disc, and which is opposed by a low ridge and indications of a double furrow on the opposite side of the central disc. Sprigg (1947, 1949) reconstructed this as two of four paired radial canals at right angles, but evidence of the other two is lacking and the significance of this character is uncertain. A feature which has not been described is the faint radial furrowing extending towards the centre from the concentric furrow at mid-radius (*vide* Glaessner 1962, pl. 1, fig. 3). This is not present around the full circumference.

As the size, proportions, and main features of *Beltanella* are within the range of similar structures in *Ediacaria*, their distinctiveness hinges mainly on the presence in *Beltanella* of the 'ring' of bosses which have been considered as possible gonads. The slab on which the *Beltanella* occurs is exceptionally rich in medusoids; eight small specimens of *Cyclomedusa* (including two clumps of three each) and two other medusoids occur, besides many vague markings. There are very few places on it where so large an individual as the holotype of *Beltanella* would not over- or underlie some other specimen. The bosses, as Sprigg noted from the first, have concentric furrows on them. A small group of *Cyclomedusa* specimens superimposed on the holotype would satisfactorily explain both this structure and the distribution of bosses (Glaessner 1962, pl. 1, fig. 3), which does not fit the interpretation of eight regularly distributed gonads. On present evidence it is not possible to prove conclusively whether these bosses are *Cyclomedusa* specimens or parts of *Beltanella*. The discovery of one or more specimens showing such bosses on slabs not rich in *Cyclomedusa* would be a strong indication of the distinctiveness of *Beltanella* but in their continued absence the taxon must be regarded as doubtful and as a possible synonym of *Ediacaria*.

Genus MEDUSINITES gen. nov.

Type species. Medusina asteroides Sprigg 1949.

Characters of type species. This genus resembles *Protolyella* only in its smooth central area, but the surrounding outer ring lacks the numerous, close-set, irregular, radial grooves and ridges. '*Medusina*' *filamentis* Sprigg does not belong here but is connected with *Pseudorhizostomites howchini* Sprigg by transitional forms. *Medusina* Walcott 1898 is an objective synonym of *Spatangopsis* Torell 1870, a form unrelated to *Medusinites*.

Medusinites asteroides (Sprigg) 1949

Plate 97, figs. 1-5

- 1949 *Medusina asteroides* Sprigg, p. 90, pl. 3, fig. 3, text-fig. 7c.
- 1949 ?*Medusina mawsoni* Sprigg, p. 89, pl. 13, fig. 4, text-fig. 7b.
- 1956 *Protolyella asteroides* (Sprigg), ?*P. mawsoni* (Sprigg); Harrington and Moore, *in* Moore, p. F155, fig. 127 (1), ?(2).
- 1959 *Protolyella asteroides* (Sprigg), ?*P. mawsoni* (Sprigg); Glaessner, *in* Glaessner and Daily, p. 381.

Material and preservation. About 20 casts on the lower surfaces of quartzite slabs, many with counterpart moulds.

Dimensions. Specimens with diameters from about 1 to 5 cm. can be identified. Smaller and slightly larger specimens lacking distinctive characters may also belong here.

Diagnosis. Small circular bodies with a very narrow, generally distorted, marginal flange surrounding a large outer ring separated from a central disc by a deep annular furrow. The radius of the central disc is smaller than the width of the outer ring. Radial furrows may be preserved on it. Faint concentric markings are more common on the central disc than elsewhere.

Remarks. In closely similar medusae, even on the same rock-surface, the marginal flange may be fully displayed, partly folded below the specimen (as in the holotype of *M. asteroides*) or absent. Specimens without a flange and with a large central disc are not clearly distinct from *Medusina mawsoni* Sprigg and it therefore seems on present evidence that this form should be merged with *M. asteroides*. It is preferable to retain the name of the form which shows most distinguishing characters, and suppress *mawsoni* as a synonym.

Genus CYCLOMEDUSA Sprigg 1947

Type species. *Cyclomedusa davidi* Sprigg 1947.

1947 *Cyclomedusa* Sprigg, p. 220.

1949 *Cyclomedusa* Sprigg, p. 91.

1949 *Madigania* Sprigg, p. 93.

1949 *Tateana* Sprigg, p. 86.

1956 *Cyclomedusa* Sprigg; Harrington and Moore, in Moore, p. F153.

1956 *Ediacaria* Sprigg (*partim*); Harrington and Moore, *ibid.*, p. F74, fig. 60 (4-5).

1956 *Madigania* Sprigg; Harrington and Moore, *ibid.*, p. F154.

1958 *Spriggia* Southcott [= *Madigania* Sprigg 1949, *non* Whitley 1945], p. 59.

1959 *Cyclomedusa* Sprigg; Glaessner, in Glaessner and Daily, p. 378.

1959 *Spriggia* Southcott, *Tateana* Sprigg; Glaessner, *ibid.*, p. 388.

Remarks. *Cyclomedusa radiata* Sprigg differs from the type species in its central boss-and-ring structure and more widely spaced deep radial furrows, with fewer concentric grooves. In several specimens of *Cyclomedusa*, however, the radial structures agree with typical forms of *C. radiata* but extend further toward the centre, which is developed as in *C. davidi*. *C. gigantea* Sprigg is represented only by its holotype, which is badly

EXPLANATION OF PLATE 97

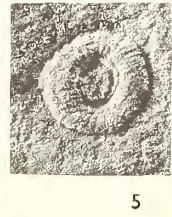
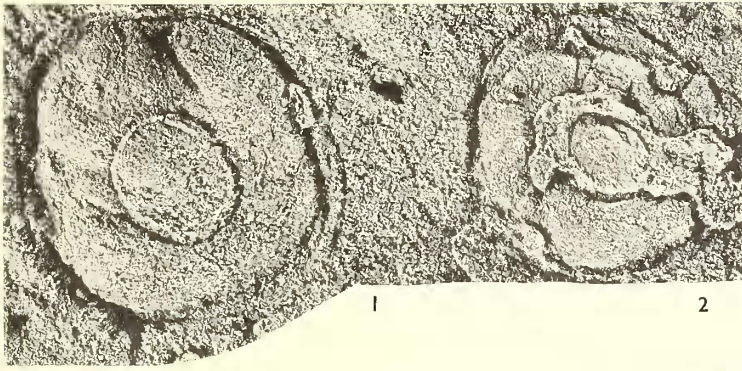
All figures $\times 1$.

Figs. 1-5. *Medusinites asteroides* (Sprigg). 1-2, hypotypes, P13785-6, showing central disc, main annular furrow, outer ring, and marginal flange. 3, holotype, T40-2021, showing also few radial furrows. 4, holotype, T39, of '*Medusina mawsoni*' Sprigg. 5, hypotype, P13783, with numerous radial furrows on outer ring.

Figs. 6-7. *Kimberia quadrata* gen. et sp. nov. 6, holotype, P12734. 7, paratype, P12739. The deep groove x-y is probably accidental rather than structural. Outlines marked where only faintly recognizable on the specimens.

Fig. 8. *Ovatoscutum concentricum* gen. et sp. nov. Holotype, P13770. Arrow points to notch, centre, and radial suture. It ends where a faint discontinuity in the rock surface sculpture may indicate the edge of a smooth portion of the disc across the notch.

Fig. 9. *Tribrachidium heraldicum* Glaessner. Hypotype, F17021. A distorted natural mould showing impressions of bristles.



weathered in the centre. Its specific distinctness from the type species is therefore questionable. The presence of areas with radial furrows on several specimens formerly placed in *Spriggia annulata* (Sprigg), including the holotype, makes its separation from *C. davidi* impracticable because of intergrading.

Cyclomedusa plaua sp. nov.

Plate 98, figs. 1–3

1959 'Unidentified medusoid fossils', Glaessner, in Glaessner and Daily, pl. 45, fig. 2 (*partim*).

Material and preservation. 8 specimens, casts on the lower surfaces of quartzite slabs.

Holotype. P13778. *Paratypes.* P13779, P13780.

Diagnosis. Adult distinguished by a broad, flat disc (maximum known radius 12 cm.) surrounding a small, central, concentrically rugose cone rarely over 1 cm. in radius; radial furrows very fine when present. The central cone is sometimes duplicated by twinning.

Remarks. *C. plana* is distinguished from *C. davidi* in adult specimens by its smaller central cone and large disc with few or without concentric rugosities, and by its finer radial striations. The fineness of these, and the central cone, differentiate it from *C. radiata*.

Genus MAWSONITES gen. nov.

Type species. *Mawsonites spriggi* sp. nov.

Characters of type species. This genus is named after the late Sir Douglas Mawson, geologist and explorer, who inspired and led his students and colleagues in the study of the Flinders Ranges and the Ediacara area.

Mawsonites spriggi sp. nov.

Plate 99, figs. 1, 2

1958 'Unnamed jellyfish', Sprigg, in Best, pl. 6, fig. *b* (figured only).

Material. Four casts on the lower surfaces of quartzite slabs. The holotype retains an elevation of 5 mm. from the rock surface in places. The paratype and other specimens are flattened.

Holotype. F17009. *Paratypes.* F17016, F17019.

Dimensions. Diameter of holotype 110–125 mm., of paratype F17016 89 mm. (maximum), of paratype F17019 64–72 mm.

Diagnosis. Large, compressed, but in life presumably dome-shaped, becoming steeply conical near centre. Central conical part smooth-walled, truncated, and compressed in curved, overlapping folds in the holotype. The greater part of the surface is strongly sculptured with arcs of prominent, large, irregular, bosses which increase in size outwards, and merge into the peripheral zone which is dominated by large, irregular, radially elongate lobes separated by deep clefts. They form radial furrows on the outer half of the disc. Periphery lobate. A circular area bearing the conical centre and the enclosing one or two arcs of bosses was more compressible than the remainder of the bell and was enclosed by a shallow annular groove on the surface of the dome.

Remarks. The peculiar distribution of large bosses on the main body of the bell, and the lobate margin, set this form apart from other fossil and living medusae. The bosses must have been fairly solid to make such well-defined impressions in the underlying sediment. In its possession of a truncate, easily compressed, possibly hollow central cone with arcuate folds in its walls *Mawsonites* approaches *Cyclomedusa davidi* and *C. plana* in the Ediacara fauna, and the Stauromedusae among modern forms.

Genus CONOMEDUSITES gen. nov.

Type species. *Conomedusites lobatus* sp. nov.

Characters of type species.

Conomedusites lobatus sp. nov.

Plate 99, figs. 3, 4

Material and preservation. Three specimens, casts on the lower surfaces of quartzite slabs.

Holotype. P13789. *Paratypes.* P13788, P13790.

Dimensions. Diameter of holotype 21–22 mm., height 1.5 mm. Diameter of paratypes P13788 and P13790 15–18 and 19 mm. respectively, height 3 and 1 mm. respectively. It should be noted that the marginal flange is obscured in P13788.

Diagnosis. Small, convex body, composed of four almost equal lobes, delimited by sharply defined grooves that deepen outwards, separating adjacent lobes at the periphery, or above a broad, distorted, marginal flange with an entire margin. Further lobes may be intercalated peripherally by bifurcation of the four apical grooves.

Remarks. Only the aboral side of *C. lobatus* is known. It is distinguished by its conical shape from the exumbrellar view of the simpler specimens of *Brooksella alternata* Walcott (1898, pl. 1, fig. 4; re-figured by Harrington and Moore, in Moore 1956, fig. 11, 2a–c). There is no reason to assume that it was a related form as there is no trace of subumbrellar lobes. A resemblance to the Ordovician *Conchopeltis alternata* Walcott, a large, low, conical, tetramerous, presumably chitinous shell for which Moore and Harrington (in Moore 1956, pp. F32, F57) erected a new Family and Suborder in the Order Conulariida, could be fortuitous, for the marginal flanges preserved in two of the three specimens are apparently entire. *Conomedusites* is the only medusoid fossil from Ediacara with a clearly displayed tetrameral symmetry.

Genus LORENZINITES gen. nov.

Type species. *Lorenzinites rarus* sp. nov.

Characters of type species.

EXPLANATION OF PLATE 98

Figs. 1–3. *Cyclomedusa plana* sp. nov. 1, paratype, P13779, $\times 1.2$. 2, holotype, P13778, $\times 1$. 3, paratype, P13780, part of specimen with twinned centre, $\times 0.75$. All specimens show the concentrically rugose small central area. Strong radial grooves in 1 and 3 are probably accidental.
Fig. 4. *Spriggina? ovata* sp. nov. Holotype, P13754, $\times 4$.



4



3



2

Lorenzinites rarus sp. nov.

Plate 100, fig. 1

Material and preservation. A single specimen, an external mould on the base of a quartzite bed.

Holotype. P13784.

Dimensions. A disc with a diameter of 5–6 mm., surrounded by eleven radiating lobes 2–3 mm. long.

Diagnosis. A small central disc from which lobes (eleven in the only known specimen) radiate, broadened and flattened at the tips. The tips may bifurcate. The edge of the disc describes a series of arcs from the base of each lobe to the base of its neighbouring lobes.

Remarks. At first glance this structure resembles the problematic medusoid genus *Lorenzina* but its lobes expand at the periphery of the fossil instead of being rounded off, and may bifurcate. Only eleven lobes are known. In this it resembles *Palaeosemaeostoma* Rüger, from the German Middle Jurassic, a genus classified as ?Trachylinida *incertae sedis* by Harrington and Moore (*in* Moore 1956, p. F76), but it lacks the raised narrow collar around the centre of the disc.

Like *Rugoconites enigmaticus* sp. nov., but unlike the other medusoid fossils which are casts, *L. rarus* is preserved as an external mould. This specimen resembles the centre of some specimens of *R. enigmaticus* but is much more regular. While its central disc is the size of the central ring-ridge of some specimens of *R. enigmaticus*, its lobes are smaller and more numerous than the innermost whorl of dichotomous radial ridges of this species. It is not likely to be a juvenile of *R. enigmaticus* because of their differing measurements and proportions, but it could be a related form.

Genus PSEUDORHIZOSTOMITES Sprigg 1949

Type species. *Pseudorhizostomites howchini* Sprigg 1949. Plate 103, figs. 2–4.

1949 *Pseudorhizostomites* Sprigg, p. 87, pl. 12, figs. 1, 3; text-fig. 6F–H.

1949 *Pseudorhopilema* Sprigg, p. 88, pl. 12, fig. 2; text-fig. 6E.

1949 *Medusina* Walcott (*partim*); Sprigg, p. 90, pl. 13, fig. 1; text-fig. 7D.

1956 *Pseudorhopilema* Sprigg, *Pseudorhizostomites* Sprigg; Harrington and Moore, *in* Moore, pp. F51, 52, fig. 41 (1–3).

1956 *Protolyella* Torell (*partim*); Harrington and Moore, *ibid.*, p. F155, fig. 127 (7).

1959 *Pseudorhizostomites* Sprigg, *Pseudorhopilema* Sprigg; Glaessner, *in* Glaessner and Daily, pp. 381–2.

Material. Over 80 specimens, most of which are impressions on the bases of quartzite slabs; and occasional counterpart casts found on upper surfaces. The following descriptions are based on the impressions.

Description. The specimens are extremely variable in appearance. Although the small number available to Sprigg (1949) could be grouped in three apparent genera, such grouping is no longer practicable for the many intermediate and new forms which are now known.

The specimens, mostly under 7 cm. in diameter, consist of furrows which radiate outwards from a centre of variable shape. As they radiate, they split and become shallow,

forming a zone of numerous very small furrows at the outer limits of many specimens. Only one specimen possesses a definite outer edge, a sharp groove preserved around half its circumference. Radial splitting and dendritic branching of the furrows are extremes of variation (Sprigg 1949, pl. 12, figs. 1-3; pl. 13, fig. 1).

Some rock specimens have been split vertically across these fossils accidentally, and others intentionally. In every example in which the lamina of quartzite immediately above the specimen had appreciable thickness (9 specimens) there were indications of post-depositional disturbance of sand grains above the centre, or above the deepest furrows. Plate 103, figs. 2-4 shows a specimen which has been split along a linear central furrow towards which all its other furrows converge. The main converging furrows can be traced into vertical flutes on the sides of a smooth-walled passage through the overlying lamina of quartzite. This passage ends on the next bedding plane. Although compaction during diagenesis has forced its sides into contiguity, the individual sand grains do not interlock. Another specimen with a linear central furrow shows a similar passage, while three with point-centres show very narrow, funnel-shaped lines of disturbance vertically above their centres, and more obscure disturbances are found in specimens with ill-defined centres or circular central furrows. All seem to have resulted from the escape of material from a decaying organism. The circular central furrows delimiting one to several rounded bosses of quartzite (e.g. '*Medusina filamentis*' Sprigg 1949, pl. 13, fig. 1) seem to result from the subsidence of the overlying sand-lamina during the escape of the organic matter, rather like the subsidence of the core of a ring-dyke. Forms such as that figured here and by Sprigg (1949, pl. 12, fig. 1, the holotype of *Pseudorhizostomites howchini*, and fig. 3b, *Pseudorhizostomites sp.*), which are more or less radial structures, seem to have been shaped largely by viscous flow towards the centre. These are the majority (over 40 specimens). The rather regular dichotomously branched form *Pseudorhopilema chapmani* Sprigg (Sprigg 1949, pl. 12, fig. 2) occurs in such numbers (about 20) that there is a possibility that some surface structures of the organism, in addition to post-mortem processes, influenced their formation.

While *Pseudorhizostomites howchini* is thus primarily based on a peculiar state of preservation of a decaying organism, it is unlikely to have been formed by the decay of any of the other medusoid organisms here described, with the exception, perhaps, of *Rugoconites*. It is likely to represent a morphologically distinctive though imperfectly known taxon. Reliable specific distinctions cannot be made within it at this time.

Genus RUGOCONITES gen. nov.

Type species. Rugoconites euigmaticus sp. nov.

Characters of type species.

EXPLANATION OF PLATE 99

Figs. 1, 2. *Mawsouites spriggi* gen. et sp. nov. 1, holotype, F17009. 2, paratype, F17016, $\times 1$. The smaller specimen is less strongly sculptured but the basic pattern is the same.

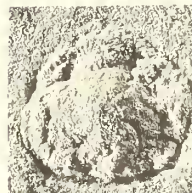
Figs. 3, 4. *Conomedusites lobatus* gen. et sp. nov. 3, holotype, P13789. 4, paratype, P13788, $\times 1$.

Fig. 5. *Tribrachidium heraldicum* Glaessner. Latex cast of holotype, P12898, $\times 1$.

Fig. 6. *Ediacaria flüdersi* Sprigg. Hypotype, F17039, showing smooth outer ring and flattened central disc, marked only by an elliptical annular furrow, $\times 0.5$.



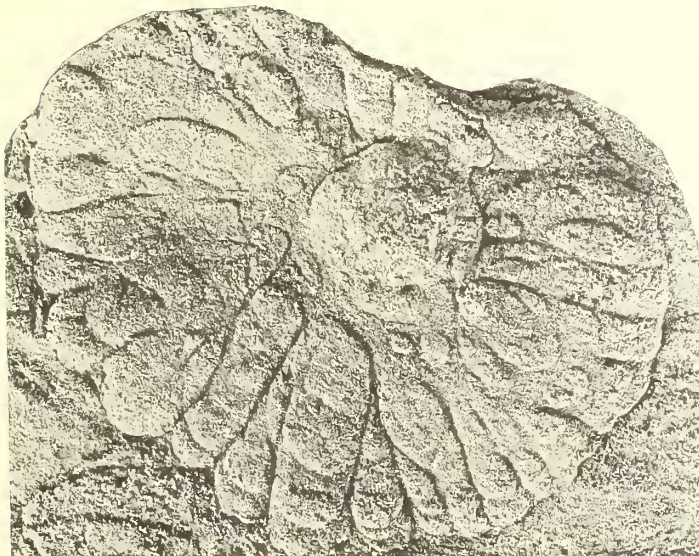
5



3



4



2



6

Rugoconites enigmaticus sp. nov.

Plate 100, figs. 2, 3

Material and preservation. 16 impressions in the bases of quartzite flags. Large impressions are relatively (and often actually) flatter than small specimens and their inner parts are obscured by flattening. The following descriptions are based on latex casts of the impressions.

Holotype. P13781. *Paratype.* P13782.

Dimensions. The smallest specimen is 16 mm. in diameter; the largest, slightly oval, has an average diameter of 64 mm.

Diagnosis. Periphery circular to oval. A few radial ridges diverge from a small central elevation or polygonal ridge, and branch dichotomously one to three times. The last dichotomy is, in each individual, a constant distance inside the periphery, and the resultant ridges curve slightly to meet the periphery at a right angle.

Remarks. In its general form of dichotomous grooves in the rock surface *R. enigmaticus* resembles *Pseudorhopilema chapmani* Sprigg (1949). It differs from Sprigg's specimen and others since collected in usually having a definite periphery and in being much more regular in its branching. The branches ('ridges', as here described, corresponding to the 'grooves' of *P. chapmani* Sprigg 1949) are much thicker in the new form, and do not taper at their outer ends but are cut off sharply at, or just within, the periphery.

Genus KIMBERIA gen. nov.

Type species. *Kimberia quadrata* sp. nov.

Characters of type species. The genus is named after Mr. John Kimber, student, teacher, and collector who lost his life during an expedition to Central Australia in 1964.

Kimberia quadrata sp. nov.

Plate 97, figs. 6, 7

1959 'Problematic fossil, possibly belonging to the Siphonophora', Glaessner, *in* Glaessner and Daily, p. 391, pl. 47, fig. 9.

Material. Four nearly complete and two fragmentary specimens are known. All are very flat casts on the bases of quartzite slabs. Some portion of each specimen is broken off at the edge of the rock.

Holotype. P12734. *Paratype.* P12739.

Dimensions. Length of holotype 65 mm., width 36 mm.

Diagnosis. Ovate bodies, rounded at one end and with a smooth contour; internal structures represented by several longitudinal, distinct zones of two kinds, coarsely segmented or with fine, transverse, frill-like grooves bordering a smooth area.

Remarks. The bodies appear to have had the shape of a narrow bell which tapered a little more towards one truncate and presumably open end than at the opposite, rounded end. All are flattened and distorted in various ways, the truncate end of the bell being noticeably less resistant to compression than the rounded end. All known specimens have a frilled zone displayed centrally with segmented zones on either side. This suggests that the bells were either flattened at the frilled zones (squamish in life) or that the segmented zones supplied resilience so that the bodies preferentially lay on the area

between two segmented zones. In this position the segmented zones would overlies one another and no specimen unequivocally shows how many there are, but there were more than two and no more than four. This seems the most probable number, as three segmented zones would not result in the frilled zone being displayed centrally. Even the two fragmental specimens seem to have been preserved in this position.

Various interpretations of the shape of this peculiar organism in life are possible. One line of argument leading to a tentative structural assessment is presented here. There is an obvious resemblance between the segmented zones of this species and the long gonads on four radial canals in some present-day medusae. These are principally found among the Carybdeida, Trachymedusina, and Leptomedusae. The gonads of the Carybdeida are paired, more lamellar, and less like tubes segmented by intermittent transverse creases than the segmented zones of *K. quadrata*; they are positioned in the corners of a more or less quadrate bell. The general shape of *K. quadrata* could have approximated that of *Carybdea marsupialis* Peron and Lesueur (Mayer 1910), but the segmented zones more closely resemble the gonads of, for example, adult Laodiceidae (Leptomedusae), which run from the stomach almost to the margin of the bell. It is difficult to relate the appearance of the frilled zone to these resemblances to structures of present-day medusae. Too little is known to justify the allocation of *K. quadrata* to one or other of the Leptomedusae, Trachymedusina, or Carybdeida, though the existence of most of its characters in one or more of these groups indicates its medusoid affinities.

Genus OVATOS CUTUM gen. nov.

Type species. Ovatoscutum concentricum sp. nov.

Characters of type species.

Ovatoscutum concentricum sp. nov.

Plate 97, figs. 8

Material. One external mould, flattened and showing some wrinkling but no fracturing. It is described from a latex cast.

Holotype. P13770.

Dimensions. Length 6.2 cm., width 6.1 cm. 35–40 concentric ribs.

Diagnosis. A large, rounded shield sculptured with strong concentric corrugation, which weakens adjacent to a triangular notch, where the outline of the shield is indistinct in the only known specimen. The centre of the sculpture, a minute, smooth, oval, convex area, is situated at a distance of about one-third of the length of the shield measured from a line across the extreme ends of the notch. The contour of the ribbing changes from

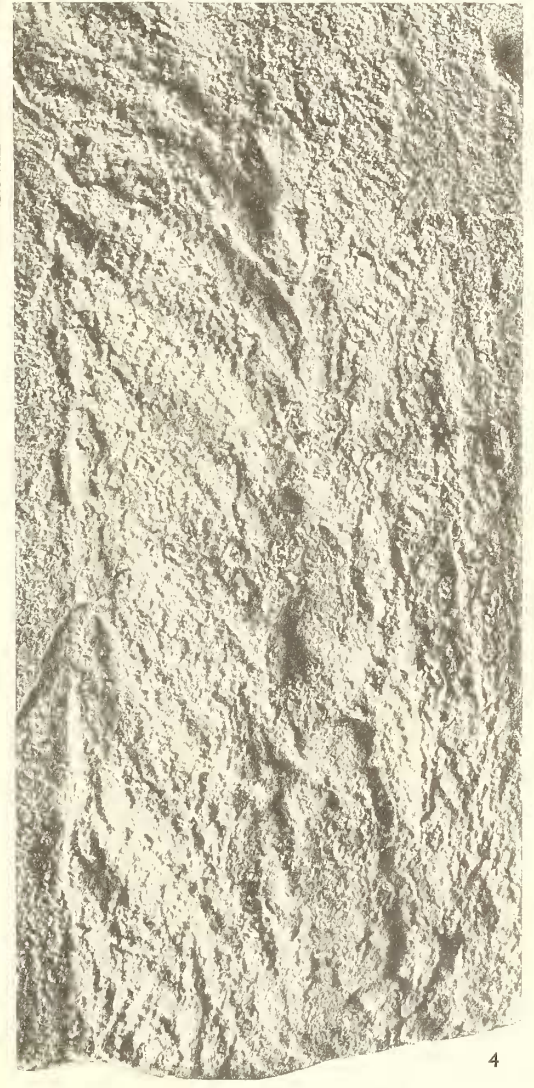
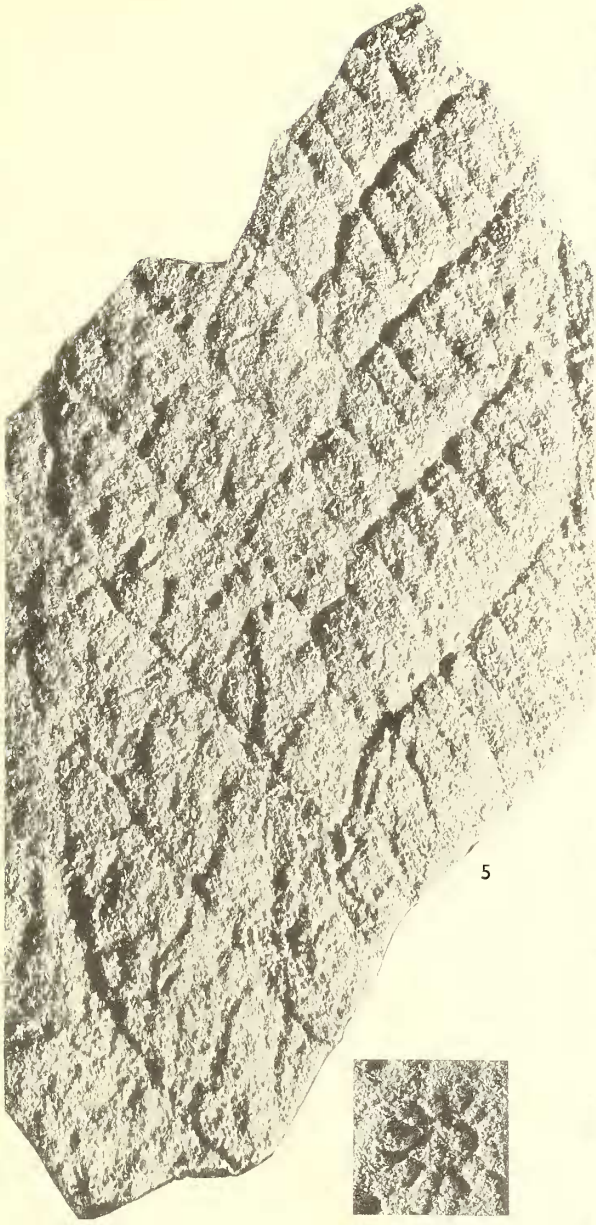
EXPLANATION OF PLATE 100

Fig. 1. *Lorenziites rarus* gen. et sp. nov. Holotype, P13784, $\times 1.5$.

Fig. 2, 3. *Rugoconites enigmaticus* gen. et sp. nov. 2, holotype, P13781. 3, paratype, P13782, one half broken off. Broken line marks faint outline of disc. $\times 1$.

Fig. 4. *Rangea longa* sp. nov. Holotype, P13777, $\times 1$.

Fig. 5. *Rangea grandis* sp. nov. Holotype, P12897, $\times 1$.



distinctly elongate at a length of 2–2.5 cm. to almost equal in length and width, but it becomes sinuous rather than circular. A suture-like zone about 1 mm. wide extends through the centre from the tip of the notch towards the opposite margin.

Remarks. The shape, sculpture, and outline of the disc are somewhat distorted in the anterior portion, apparently through draping over an irregularity of the underlying surface. The ribs become wider and possibly more widely spaced towards the periphery. In some places they appear to be asymmetrical in profile, sloping more steeply towards the centre. The only radial lines are the suture-like zone where the profile of the ribs appears to be flatter and more evenly convex, and the edges of the notch, where the sculpture disappears along irregular and frayed-looking boundaries which are convex towards the median line. The notch does not extend to the centre.

The fossil is strikingly similar in outline and sculpture to *Plectodiscus cortlandensis* Caster, from the Upper Devonian of New York State (Caster 1942). It is only half as large as the holotype of this species and lacks the central cone described in much detail by Caster. He does not mention any notch but the sculpture appears to be absent in a triangular area between F and I (Caster 1942, pl. 1, fig. 1), corresponding in position to the notch in *Ovatoscutum*. The original substance of *P. cortlandensis* was described as 'tough and flexible'. This would also fit *O. concentricum*. Caster described the grooves between the ribs as 'asymmetrical, the steeper slope being consistently peripherad'.

P. cortlandensis was interpreted by Caster, as a result of detailed though 'speculative' interpretation, as a velellid float (pneumatophore). He examined other possibilities, such as an affinity with brachiopod shells, but found only superficial resemblances. Superficially, *Ovatoscutum* may also be thought to resemble a brachiopod shell, but it must have been quite flat, as the sculpture is not much distorted. The notch is unlike any brachiopod structure. The possibility of the suture-like zone being a hinge of a bivalved shell was also considered, but there is no discontinuity across this zone. Much of Caster's interpretation is concerned with proof of the existence of a 'sail' in *Plectodiscus*. No evidence of such a structure exists in *Ovatoscutum* which, if correctly identified as a pneumatophore of one of the Hydrozoa Chondrophorina, would have resembled that of the living *Porpita* rather than that of *Velella*. Harrington and Moore (*in* Moore 1956, p. F149) gave the following diagnosis of the Family Porpitiidae Brandt, 1835: 'Corm highly vaulted or flattened disc-like, without crest or sails.' Ordovician to Devonian disc-like fossils assigned to this family have at least some radial sculptural elements. In this respect the new genus differs from all Porpitiidae but this does not necessarily affect its tentative interpretation as a chondrophoran pneumatophore.

B. Pennatulacean Fossils

The interpretation of the genera *Rangea*, *Pteridinium*, and *Charnia* as representatives of the Order Pennatulacea (Anthozoa Octocorallia) was discussed in previous publications to which reference is made in the following systematic descriptions. New material confirms this assignment but does not yet permit a classification at family group level. The family Pteridiniidae Richter 1955 was based on a genus which is still incompletely known. It is not advisable to re-define it at this stage. The material from Ediacara which was previously placed in the species *Rangea arborea* Glaessner can now be separated into a species of *Rangea* (not including the holotype of *arborea*) and

another species. Its markedly different characters had been considered earlier, on the evidence available from a limited number of specimens, as the result of post-mortem alteration of *Rangea*. The description of the genera and species now known requires a revision of descriptive terminology. For those genera which are close to Pennatulidae the terms applied to living forms can be used, although no polyps are discernible. But other genera deviate from living pennatulids and require new descriptive terms.

The body of all these fossils consists of a *rhachis* from which a leaf-like expansion (*frond*) spreads with bilateral symmetry, as a plant leaf spreads from its mid-rib. The term 'leaf' is not available, however, as in living pennatulids the numerous subordinate individual ridges which spread from, or are wrapped around, the rhachis are known as *polyp leaves*. They correspond to the *primary branches* which are delimited in fossils by *primary furrows* extending laterally from the sides of the rhachis or from the mid-line. In *Pennatula* the polyp leaves are deeply separated, so that there are no primary furrows, while in *Rangea* they are free only near the periphery (text-fig. 1c). In the species *arborea* they appear to have been rising above one surface of a *foliate base* (the main part of the frond), so that the term 'primary furrow' here becomes ambiguous. It could refer to a line on either side of the basal attachment of the polyp leaf or, since the polyp leaves may be flattened against the foliate base in fossilization, it could also refer to what in life was their free upper edge. The term *basal trace* is therefore used instead of primary furrow for this structural type. In *Pteridinium*, however, the primary branches are delimited by clear-cut primary furrows. In *Rangea* and *Charnia* the primary branches are clearly divided into *secondary branches* which correspond to the *anthosteles* in Pennatulacea. Such secondary branches and delimiting *secondary furrows* are also seen on the ventral side of *arborea*, but only very rarely and faintly in *Pteridinium*. The designation of the two sides of the foliate base as *dorsal* and *ventral* is conventional, as in all Pennatulacea, the rhachis often appearing as a wide track dorsally and as a narrow zigzag line between contiguous polyp leaves ventrally. The rhachis may extend downwards (in the living position) into a *stalk* which in Recent forms may end in a bulbous expansion. There are fossil specimens showing a long stalk with a pennatulacean fossil (like *Charnia* Ford) at one end, but there are also similar stalks ending in a round medusoid cast (like *Charniodiscus* Ford). No unquestionable fossil with a medusa-like base and a pennatulacean upper end has yet been found.

Genus RANGEA Gürich 1930

Type species. Rangea schneiderhoehni Gürich 1930.

The relations between the genera *Rangea*, *Charnia*, and *Pteridinium* require further study. A discussion of these general problems is beyond the scope of the present contribution.

Rangea longa sp. nov.

Plate 100, fig. 4; text-fig. 1

1959a *Rangea* sp. nov. (*partim*) Glaessner, pp. 1472-3.

1959 *Rangea arborea* (*partim*) Glaessner, in Glaessner and Daily, p. 383, pl. 45, fig. 1 (only).

1962 *Charnia* sp. b, Glaessner, pl. 1, fig. 5.

Material and preservation. Twelve specimens in good to fair preservation belong here. On one bedding plane they are preserved on the upper surfaces of rock slabs (Glaessner, in Glaessner and Daily 1959,

pl. 45, fig. 1) but elsewhere they occur on lower surfaces; this is most common in all groups of fossils at Ediacara.

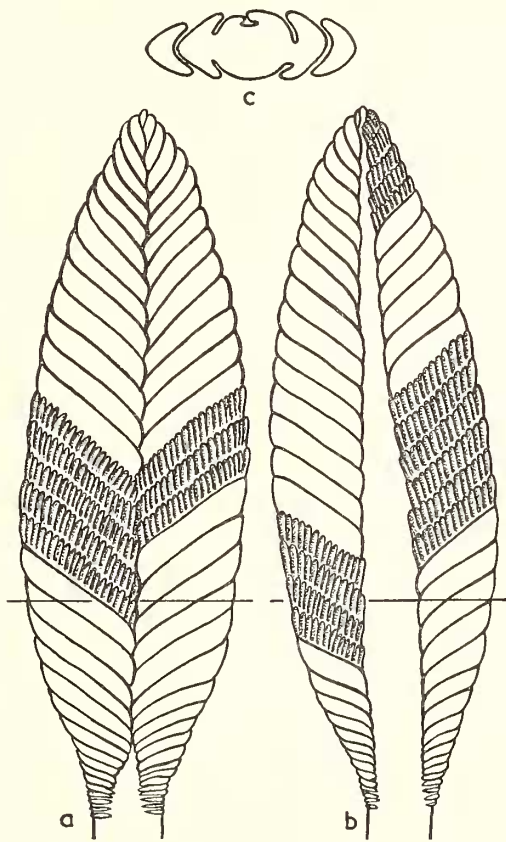
Holotype. P13777.

Dimensions. The holotype is 15 cm. long and about 6 cm. wide. The largest fragmentary specimen is 25 cm. long.

Diagnosis. Angle between axis and primary branches (polyp leaves) commonly acute, but it could evidently be modified by bending. Polyp leaves made up of secondary branches (anthosteles) of uniform appearance, elongated approximately at right angles to the free (upper) edges of the polyp leaves. The secondary branches are separated by furrows that are deeper at their upper ends. Twenty or more secondary branches in larger leaves, fewer in smaller leaves in every example.

Description. Outline of frond variable, from fusiform to very elongate. All specimens lie flat (or almost flat) on dorsal or ventral sides, indicating that their width must have exceeded their thickness prior to compression. The margins are lobate, the outwardly convex portions corresponding to the polyp leaves, and the indentations to the furrows between them. Normally these primary furrows are straight, lying at angles from 25° to 50° to the axis, the angles being steeper near the apex of the frond. The secondary furrows form approximately right angles with the upper edge of the polyp leaf. The largest number of these depressions counted is 17 but counts could not be made on complete leaves. The secondary furrows are most distinct near their upper ends, which could have divided the upper margin of the polyp leaves into separate lobes. In their position and varying degree of distinctiveness they correspond to the anthosteles of some modern pennatulids. In some specimens some secondary branches are transversely wrinkled. The width of the polyp leaves in the mid-portion of a frond is from about one-third to one-sixth of their length. Approximately 1:5 is the most common ratio.

Remarks. The most obvious differences between the type species *R. schneiderhoehni* and the Australian form are possibly due to preservation. They are the questionable 'outer flange' of the holotype of *R. schneiderhoehni* and the oblique angle which its



TEXT-FIG. 1. *Rangea longa* sp. nov. Reconstruction based on the holotype and three other specimens, $\times 0.5$ (approx.). a, ventral view; b, dorsal view; c, diagrammatic cross-section along transverse line.

secondary furrows make with the primary furrows. The African material consists, as far as we know, of only two specimens and is inadequate to elucidate which of its characters are diagnostic. No other material of this species has been obtained to date. Rather than doubtfully assign the better-known Australian material to the less well-known African species, we have described it as a new species. The holotype and other specimens from Ediacara of a species previously placed in *Rangea* can now be distinguished generically from *R. schneiderhoelmi*, on the basis of new material. Some others are placed in *Pteridinium*. One unique specimen is considered as specifically distinct from *R. longa*.

Rangea grandis sp. nov.

Plate 100, fig. 5

1959a *Charnia* sp., Glaessner, p. 1472, text-fig. 1b.

1959 *Rangea?* sp. (changed in addendum to *Charnia* sp.), Glaessner, in Glaessner and Daily, p. 397, pl. 46, fig. 2.

1961 *Charnia* sp., Glaessner, p. 75, text-fig.

1962 *Charnia* sp. a, Glaessner, pp. 484-5, pl. 1, fig. 4.

Material and preservation. One fragment of the mid-portion of a large frond preserved as a cast on the lower surface of a rock slab.

Holotype. P12897.

Dimensions of holotype. Overall length of fragment approximately 160 mm., maximum measurable width 75 mm. The longer dimension of the lowest secondary branches (anthosteles) on either side is 20 mm., decreasing fairly regularly to 14 mm. in the highest pair of polyp leaves.

Diagnosis. Frond large. Ventral zigzag furrow irregular. Primary branches (polyp leaves) make an acute angle with the axis (30°-40° in the holotype). Secondary furrows divide the polyp leaves into secondary branches (anthosteles) with bluntly rounded tips but become shallow grooves across the lower one-half to two-thirds of the polyp leaves. The secondary branches are larger and fewer than in other species; they narrow somewhat towards the outer margins of the frond, and 13 is the greatest number known in one polyp leaf.

Remarks. *R. grandis* differs from *R. longa* and from *R. schneiderhoelmi* in its much larger secondary branches (anthosteles), which are about three times as wide as the largest known in *R. longa*, and fewer in each primary branch. Diminishing width of the anthosteles away from the axial furrow has not been observed in *R. longa* or *R. schneiderhoelmi*. Like *R. longa* and unlike *R. schneiderhoelmi*, the secondary furrows of *R. grandis* are roughly at right angles to its primary furrows.

Genus PTERIDINIUM Gürich 1930

Type species. *Pteridinium simplex* (Gürich) 1930.

Topotype material of *Pteridinium simplex* was described by Glaessner (1963a).

Pteridinium cf. *simplex* (Gürich)

cf. 1929 'Nr. 1', Gürich, p. 85.

cf. 1930a 'Nr. 1' Gürich, pp. 671, 680, fig. 1.

cf. 1930b *Pteridinium simplex* Gürich, p. 637.

- cf. 1933 *Pteridinium simplex* (Gürich); Gürich, p. 144, fig. 4a-c.
 cf. 1955 *Pteridinium simplex* (Gürich); Richter, p. 246, pl. 1-6, pl. 7, fig. 11.
 ?1959 *Pteridinium* sp., Glaessner, in Glaessner and Daily, p. 382, pl. 46, figs. 3, 4.
 cf. 1963 *Pteridinium simplex* (Gürich); Glaessner, p. 113, pl. 1, pl. 2, fig. 1.

Material and preservation. Two small and obscure specimens (P12744a, b, described in Glaessner 1959a), and four or five fragmentary larger specimens (collected 1964 by M. Wade). One of these (F17010A-C) is preserved as a generally convex cast (A) showing two fragments of a frond, with their median zones forming approximately a right angle. The margins of the larger fragment are obscured but appear to converge away from the smaller one which has the margins curled down giving a polygonal outline. There is a counterpart or natural mould (B) of this specimen, generally concave, showing the features of A in mirror image. A small piece of rock (C) was removed from this counterpart block. It shows a continuation of the larger fragment of A extending for 10-20 mm. along the median zone and actually overlying the left-hand side of the smaller specimen by about 10 mm. vertically. The two specimens could represent two individuals overlapping accidentally, or two fragments of the same individual. The other three specimens are convex casts, without counterparts. Two show short fragments of one side of the frond without the median zone. The lateral margin is preserved in one of them. The third fragment shows a short portion of the median zone and part of one lateral margin. As in the Nama quartzite from South-west Africa, the specimens are contorted and they are found on surfaces fractured by weathering. Only very small areas can be freed by further mechanical preparation.

Dimensions. The larger fragment of F17010 is about 80 mm. long, with a maximum width of about 55 mm. The smaller fragment is about 35 mm. long and up to 45 mm. wide. The other specimens are 48, 45.5, and 42 mm. The distances between primary furrows are 4-4.5 (F17010), 5.4, 2.3-3.5, and 5 mm.

Occurrence. Remains of *Pteridinium* were first recorded from the fossiliferous flaggy quartzites. Others have since been found in a massive quartzite on a low hill top about 3000 ft. north-north-east of the southernmost outcrop of these beds, some 60 ft. stratigraphically below the main fossiliferous beds. At this locality the rock outcrop is affected by later silcrete formation during weathering. *Pteridinium* is the only fossil found here.

Remarks. The new material from Ediacara obviously represents one species. The two specimens described earlier from the richly fossiliferous beds can be included in it only doubtfully, because of poor preservation. This material has been compared in detail with *P. simplex* from the Kuibis Quartzite of South-west Africa, as represented by about 18 specimens described by Richter (including the neotype of which a cast is available to us), 8 specimens lent by the Geological Survey of South Africa, and 8 specimens lent by the Museum of South-west Africa. Thirty-four specimens of this species are now known.

The characters of *P. simplex* and their variability have been comprehensively described by Richter (1955), who gave careful attention to the influence of peculiarities of preservation on the appearance of these fossils. Little can be added to his observations. Some additions, based on the South African Geological Survey material (Glaessner 1963) can be summarized as follows: (1) The presence of secondary furrows between the primary furrows, noted by Gürich but questioned by Richter, has been confirmed on one specimen. (2) The interpretation of the course of the primary furrows as 'forward and outward' as proposed by Richter has been questioned and a more transverse course with distal convexity assumed. Admittedly, this is still hypothetical and the true position of the proximal end has not been established beyond doubt in any specimen. (3) A broad (5 mm.) median zone was found in one specimen (No. 1), instead of the median narrow zigzag line, but here again there is no confirmation from other specimens. The removal of a piece of quartzite at the lower end of this specimen (as figured on pl. 2, fig. 1, Glaessner 1963) has revealed a part of a convex cast 70 mm. long along the

median zone. Its lateral zone is separated from that of the originally described concave mould by up to 7 mm. of rock. This could be a 'lower surface' (as in Richter's pl. 2, fig. 3 and pl. 4, fig. 5c, x-x), but no less than four other interpretations of this specimen are possible, based on varying assumptions of folding-over and subsequent loss by erosion or lithification of half-specimens, as described in some of Richter's specimens in which duplication by apposition has occurred. Some of these interpretations would make it doubtful whether the broad median zone now visible on the mould is an original character of a single specimen. Two of the new specimens from Ediacara and five of the eight specimens of *P. simplex* from the Museum of South-West Africa again show only a narrow median zigzag line; in the others this region is not preserved or not clearly visible.

The material from Ediacara, like that from South-West Africa (with the one possible exception mentioned) shows identical aspects of *Pteridinium*, consisting of a leaf-shaped surface with a median zone developed as a narrow zigzag line from which primary furrows extend laterally, with slightly staggered placing of their origins. Measurements of the spacing of these furrows indicate a slightly greater width (5.0, 5.4 mm.) in two of the Ediacara specimens than in the African material, in which 4.7 mm. seems to be the widest and about 2 mm. the narrowest. No gradients of spacing along the frond length have been observed and too few reliable widths of fronds to which spacings could be related are observable to be significant for comparison. Another possibly diagnostic character of the Ediacara material is a convergence of primary furrows (and narrowing of primary branches) towards the margins of the fronds. This, however, was observed only on 5-6 primary branches, while others give only a general impression of greater curvature. The distinction between inner and outer lateral zones is weaker than in some South-West African specimens but this is a variable character.

The distinguishing characters of the few specimens of *Pteridinium* from Ediacara do not appear to be sufficiently diagnostic from those of the much more abundant material of *P. simplex* to establish a new species.

The interpretation of *Pteridinium* rests largely on its similarity with *Rangea* and *Arborea*. Richter had referred both forms to the Gorgonacea, assuming that the frequently observed apposition of specimens was indicative of the diagnostic branching of fronds in this group. The large number of specimens of *Pteridinium* now known, without a single branching one among them, disposes of his argument. Richter also concluded from the apposition and from the apparently sediment-infilled specimens that *Pteridinium* had a 'lower' surface which was virtually identical with the upper surface and in which ridges rising upwards corresponded in position to grooves, and depressions to the upwardly convex primary branches. This remains questionable. Alternatively, the 'lower' surface could have been featureless and perishable, leaving essentially an 'upper' lamina as the only potential fossil to represent a former somewhat *Renilla*-like organism.

Genus ARBOREA gen. nov.

Type species. Rangea arborea Glaessner 1959.

Diagnosis. Dorsal track broad, ventral track narrow to fairly broad, zigzag-shaped; rhachis extends downwards to form a stalk ending probably in a basal expansion. The rhachis extends laterally into a thin, smooth, foliate base forming a frond with

entire margins. Lateral primary branches can be seen as ridges on both ventral and dorsal sides of the foliate base, but they do not project as much on the dorsal side as they do ventrally. The mainly ventral attachment of the foliate base to the rhachis produces in less compressed specimens triangular pocket-like hollows between the rhachis and each of the primary branches on the dorsal side. Flange-like polyp leaves showing grooves (secondary branches), apparently delimiting fused anthosteles, arise from each basal trace. They are probably confined to the ventral side and end before reaching the margin or on it. Their preservation in varying positions indicates that their free edges extended away from the foliate base in life. Sharp, straight, linear grooves on the rhachis ('median field') and primary branches can be interpreted as impressions of spicules.

Remarks. Abundant new material has led to a reinterpretation of the pennatulacean fossils from Ediacara. The forms with pronounced spicular impressions, formerly considered as distinguished from typical forms of *Rangaea* mainly by their state of preservation, also possess flange-like and flexible primary branches which do not reach the leaf margins.

Arborea arborea (Glaessner) 1959

Plate 102, figs. 1, 2; text-fig. 2

1959a *Rangea* sp. nov. (*partim*) Glaessner, pp. 1472-3.

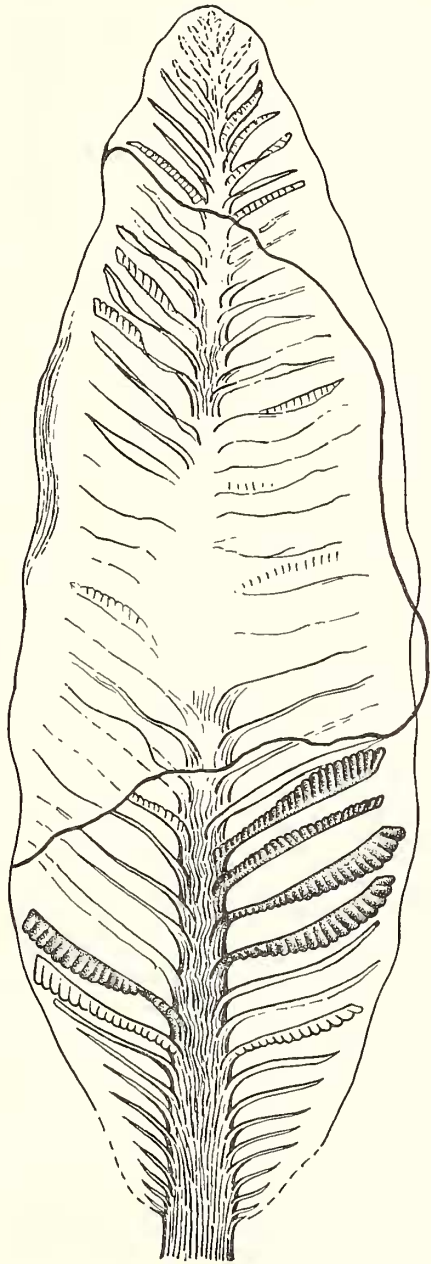
1959 *Rangaea arborea* Glaessner, in Glaessner and Daily, p. 383, pl. 43, figs. 1-3, ?fig. 4; pl. 44, figs. 1-3; pl. 45, fig. 2 (part), ?pl. 46, fig. 1.

Material. 35 specimens.

Dimensions. The incomplete holotype (P12891) measures 15 cm. along the axis. Its greatest measurable half-width is 5.5 cm. The largest known specimen is about 60 cm. long and over 10 cm. wide.

Diagnosis. Spicules in the axis lie approximately longitudinally in the dorsal track, but zigzag from side to side of the ventral track at the insertions of primary branches. In the frond, spicules are approximately parallel to the primary branches.

Remarks. The polyp leaves may be buried in a collapsed position, forming a ridge on the basal trace, with all structure blotted out, or they may



TEXT-FIG. 2. *Arborea arborea* (Glaessner). Drawing of the holotype surrounded by reconstruction based on other specimens. $\times 0.5$.

be folded flat against the foliate base, upwards (i.e. towards the apex), or downwards (towards the stem). Composite moulds show the secondary branches (anthosteles) as convex projections and the secondary grooves as furrows. They were soft enough to collapse like medusae downwards into the sediment while those of *Rangea longa* (but not *R. grandis*) usually stood up long enough to produce external moulds at the base of the overlying sedimentary layer. This supports the supposition that they are often absent because of comparatively rapid disintegration of the polyp leaves which also brings the supporting spicules to the surface to form clear-cut impressions. As the polyp leaves of *Arborea* show more clearly on the ventral than on the dorsal side of a foliate base, this genus may be compared with *Renilla*, but in this living form there is no linear arrangement of the polyps on the surface of the foliate base.

Phylum Annelida

Genus DICKINSONIA Sprigg 1947

Type species. Dickinsonia costata Sprigg 1947.

This genus, representing the Family Dickinsoniidae Harrington and Moore 1956, differs from *Spinther* in the absence of the claw-like parapodia which this living genus uses in its predatory life on sponges. *Dickinsonia* was a free-living organism, apparently moving on the sediment or in the water above it by body undulations rather than by parapodial crawling. Specimens of *Dickinsonia* are preserved as moulds or casts. There are partly decayed specimens showing frayed edges and traces of longitudinal muscles, and specimens with multiple impressions of the peripheral margin resulting from contraction after the first contact with the substratum.

Dickinsonia costata Sprigg

Plate 101, fig. 4

- 1947 *Dickinsonia costata* Sprigg, p. 221, pl. 7, fig. 2.
 1947 *Papilionata eyrei* Sprigg, p. 223, pl. 8, fig. 2.
 1949 *Dickinsonia costata* Sprigg, *D. minima* Sprigg, p. 95, pl. 18, fig. 2; pl. 19, figs. 1, 2; pl. 20, figs. 1, 2; pl. 21, figs. 1-4; text-figs. 9, 10.
 1955 *Dickinsonia spriggi* Harrington and Moore, p. 160.
 1956 *Dickinsonia costata* Sprigg, *D. minima* Sprigg, *D. spriggi* Harrington and Moore, in Moore, p. F24, figs. 13-16.
 1956 *Papilionata eyrei* Sprigg; Harrington and Moore, *ibid.*, p. F159.
 1959b *Dickinsonia costata* Sprigg, *D. minima* Sprigg; Glaessner, p. 526, fig. 4.
 1959 *Dickinsonia costata* Sprigg; Glaessner, p. 379.

EXPLANATION OF PLATE 101

- Figs. 1-3. *Pteridinium* cf. *simplex* (Gürich). 1, 2, counterpart casts and moulds of specimen F17010A-B above and possibly another specimen below. 3, same as 2 with part of cast (F17010C) which was removed in 2 to reveal underlying surface. $\times 1$.
 Fig. 4. *Dickinsonia costata* Sprigg. Hypotype, T53. Cast with faint segmental sculpture and with infilled intestinal caeca on antero-median part. $\times 1$.
 Fig. 5. *Tribrachidium heraldicum* Glaessner. Holotype, P12898, $\times 3$. As the holotype is an external mould (impression), the direction of the curvature of the three arms is reversed from that in the animal as represented by latex casts (Pl. 99, fig. 5).